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SOYBEAN GROWTH RESPONSE TO WATER SUPPLY AND ATMOSPHERIC CARBON DIOXIDE ENRICHMENT

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ABSTRACT: Growth response of soybean [*Glycine max* (L.) Merr. 'Bragg'] grown in open top field chambers at five carbon dioxide (CO_2) concentrations ranging from 349 to 946 μLL^{-1} and under two water regimes was examined. During reproductive growth, plants grown under CO_2 enrichment exhibited increases in total leaf area and dry weight. Water stress inhibited growth at all CO_2 levels, but the relative enhancement of growth due to CO_2 enrichment under water-stressed (WS) conditions was greater than under well-watered (WW) conditions. Water-stressed plants grown under 946 μLL^{-1} CO_2 were larger than WW plants grown under 349 μLL^{-1} CO_2. Reproductive yield increases were represented by increases in seed number rather than larger seeds. Although water stress reduced yield, the relative increase in seed number in response to elevated CO_2 was greater for WS plants. Leaf tissue analysis suggested that a phosphorus deficiency may have restricted the seed dry weight response to elevated CO_2. The mean relative growth rate (RGR) and mean net assimilation rate (NAR) increased with CO_2 concentration in the first interval (5 to 14 days after planting) and diminished with time thereafter for each CO_2 level. At the second interval (14 to 63 days), the direct effect of NAR was offset by lower leaf area ratio (LAR). However, the LAR was greater for WS plants but the response of RGR to CO_2 was similar under both water treatments. At the third interval (63 to 98 days), the RGR for WS plants remained constant across CO_2 treatments, whereas under WW conditions a level response of NAR coupled with a negative response of LAR resulted in a decrease in RGR under CO_2-enriched conditions. The decrease in

LAR was attributed to a decrease in specific leaf area. Leaf weight ratio was unaffected by CO_2.

INTRODUCTION

Global atmospheric CO_2 concentration is increasing (Keeling et al., 1989). Since plants respond directly to CO_2, it is important to understand how this elevated concentration will directly affect the productivity of agricultural ecosystems. Carbon dioxide enrichment frequently increases net photosynthesis, plant water use efficiency, and biomass production and yield (Rogers et al., 1993). However, in order to make reliable predictions of future crop response to elevated CO_2 concentration, it will be necessary to consider the interactions of CO_2 with other environmental factors.

Chief among these is available soil water which is a major limitation to crop production (Boyer, 1982). Annual yield fluctuations and the occurrence of water stress at critical stages of growth have been largely attributed to variations in the amount and distribution of precipitation (Turner and Kramer, 1980). Previous work has suggested potential amelioration of plant water stress by increased atmospheric CO_2 level due to partial stomatal closure (Rogers et al., 1984b; Prior et al., 1991). Reports that increased CO_2 ameliorates water stress are not uncommon (Acock and Allen, 1985; Rogers and Dahlman, 1993). Controlled environment studies have demonstrated that although water stress greatly reduces plant growth, the relative increase in total dry weight and yield of water-stressed plants in response to CO_2 enrichment were as great as under well-watered conditions (Gifford, 1979; Sionit et al., 1980; Sionit et al., 1981).

The purpose of the present experiment was to investigate the long-term effects of elevated CO_2 and water supply on soybean growth, development, and yield. Soybean plants were grown in large containers in open top chambers (Rogers et al., 1983b) under various CO_2 concentrations. Plants were subjected to repeated drying cycles for most of the vegetative period (except germination and early seedling phase) and all of the reproductive stage.

MATERIALS AND METHODS

Soybean plants were grown in open top field chambers at different atmospheric CO_2 concentrations and in open plots (no chambers) under ambient atmospheric conditions. There were two replicates of six CO_2 treatments which had a mean seasonal daytime CO_2 concentration of 348 $\pm$ 19 (ambient plots without chambers), 349 $\pm$ 19 (ambient chamber), 421 $\pm$ 22, 496 $\pm$ 24, 645 $\pm$ 33 and 946 $\pm$ 49 μLL^{-1}. Description of the CO_2 exposure system has been reported elsewhere (Rogers et al., 1983b; Prior et al., 1991)

Seeds were inoculated (Nitragin Co.)[1] and planted in 16.5-L pots containing 13 L of a 2:1:1 mixture by volume of sandy clay loam soil:sand:Metro-Mix 220 (W.R. Grace Co.). Plants were thinned for uniformity at 5, 10, and 14 days after planting, to a final density of one plant per pot. Each study plot contained 20 plants which were divided into two groups of 10 and subjected to two watering regimes. The experiment was a split plot design with a randomized complete block arrangement of the main-plot factor (CO_2 treatment) with two blocks. The treatments of the second factor (water treatment) were randomly assigned to subplots (pots) within each main plot. Differential water treatments were established by using vacuum gauge tensiometers and by erecting removable transparent plastic covering within all plots during periods of rainfall. Pots were placed on racks to insure proper drainage. Plants were rewatered when tensiometers reached -0.005 to -0.015 MPa and -0.075 to -0.085 MPa for well-watered controls (WW) and water-stressed (WS) plants, respectively. Drying cycles started two weeks after emergence when plants were at the third node stage (V-3; Ferr and Caviness, 1977). One liter of a N-free nutrient solution (Israel, 1981) per pot was added once a week for the duration of the growing season.

Plants were harvested at 14, 63, 98, and 140 days after planting corresponding to the seedling, anthesis, pod fill, and maturity stages. At each harvest, six randomly chosen plants were collected from each water by CO_2 treatment combination. Leaf area was determined photometrically and dry weights of plant parts were determined after drying at 55°C for three days. In addition, the following growth parameters were determined using classical growth analysis techniques (Kvet et al., 1971): (1) relative growth rate (RGR), the amount of dry matter produced per unit of dry matter present per unit time

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[1]Trade names and products are mentioned solely for information. No endorsement by the USDA is implied.

(kg kg^{-1} day^{-1}); (2) net assimilation rate (NAR), the amount of dry matter produced per unit leaf area per unit time (g m^{-2} day^{-1}); (3) leaf area ratio (LAR), the amount of leaf area per total plant dry weight (m^2 kg^{-1}); (4) specific leaf area (SLA), the amount of leaf area per total leaf dry weight (m^2 kg^{-1}); and (5) leaf weight ratio (LWR), the amount of leaf dry weight per total plant dry weight (kg kg^{-1}). Mean RGR and NAR were calculated for three intervals: 5 to 14 days, 14 to 63 days and 63 to 98 days. For the first interval calculations, the plant dry weight at day 5 averaged 0.144 g (mean dry weight per seed at planting) and the cotyledonary photosynthetic area averaged 3.5 cm^2.

Statistical analysis of data were performed using standard analysis of variance (ANOVA) and regression techniques (Statistical Analysis Systems, SAS Institute, Cary, NC).

RESULTS AND DISCUSSION

Growth, Development, and Yield

At 14 days after planting, low soil water availability had no effect on measured variables and therefore analyses were performed on combined WS and WW data (Table 1). The expected increase in total dry weight and leaf area due to CO_2 enrichment as reported by others (Rogers et al., 1984a; Patterson and Flint, 1980) was not found; lack of differences may be attributed to competition from other plants since a final density of one plant per pot was not attained until this harvest. Also growth from cotyledonary food supplies could dampen the CO_2 effect.

At anthesis (63 days) and pod fill (98 days), total dry weight under both water regimes was enhanced by the higher concentrations of CO_2 (Tables 2 and 3). At anthesis, dry weights of plants for the WW and WS treatments were ~88% higher when grown at 946 μLL^{-1} vs 349 μLL^{-1} CO_2, while at pod fill they were 32% and 93% higher, respectively. These results are in general agreement with data from other CO_2 studies with soybean of similar age grown under well-watered conditions (Patterson and Flint, 1980; Patterson and Flint, 1982; Rogers et al., 1983a; Rogers et al., 1984a)

At anthesis, water stress reduced total plant dry weight relative to WW control proportionately more at high CO_2 than at ambient CO_2 (Table 2). The opposite was observed at pod fill (Table 3). Despite this adverse stress effect, relative increases in total dry weight were as great or greater for water stressed plants grown under CO_2 enrichment

Table 1. Mean total dry weight, leaf area, and height for soybeans grown under two water regimes in open plots and five CO_2 treatments within chambers at 14 days after planting (well-watered = WW, water-stressed = WS).

CO_2 (μLL^{-1})	Dry Wt. (g)		Leaf Area (cm^2)		Height (cm)	
	WW	WS	WW	WS	WW	WS
348‡	0.41	0.39	43	43	6.5	6.5
349	0.39	0.36	54	50	6.9	6.8
421	0.41	0.42	55	53	6.7	7.2
496	0.41	0.46	53	57	7.0	7.2
645	0.44	0.44	54	51	6.9	7.4
946	0.51	0.44	60	55	7.2	7.0
s_x¶	0.04		3.5		0.2	
CV (%)	10.8		10.6		7.8	
b_0§	0.42		52.3		6.9	
$b_{chamber}$	NS		NS		NS	
b_{linear}	NS		NS		NS	
$b_{quadratic}$	NS		NS		NS	
R^2	NS		NS		NS	

‡ Ambient plot (no chamber).

¶ s_x and CV (%) from ANOVA.

§ Curves were fitted against actual CO_2 values. Note: Linear and quadratic coefficients and their standard errors should be multiplied by 10^{-3}.

which are in agreement with results reported for wheat (*Triticum aestivum* L.) by Gifford (1979). Others have reported that wheat plants subjected to acute water stress during early reproductive growth exhibit increases in total dry weight due to additional CO_2; however, total dry weights were reduced about equally by stress under both low and high CO_2 concentrations (Sionit et al., 1980; 1981).

Effects of CO_2 enrichment on plant height at anthesis and pod fill are shown in Tables 2 and 3. Height differences, while statistically significant, were not great at anthesis; the effect disappeared by pod fill. Height at both sampling times was unaffected by stress.

Table 2. Mean total dry weight, leaf area, and height for soybeans grown under two water regimes in open plots and five CO_2 treatments within chambers at 63 days after planting (well-watered = WW, water-stressed = WS).

CO_2 (μLL^{-1})	Dry Wt. (g)		Leaf Area (cm^2)		Height (cm)	
	WW	WS	WW	WS	WW	WS
348‡	34.3	28.9	3820	3034	60	50
349	46.5	27.0	5150	3429	77	73
421	53.5	35.1	5425	4299	78	80
496	61.8	38.6	5743	4092	78	78
645	72.4	50.2	6060	5268	84	87
946	87.6	51.0	6582	5140	81	80
s_x¶	2.4		1.2		2.4	
CV (%)	11.7		15.9		8.0	
b_0§	10.8	-23.8	3188.7	1934.6	35.1	
$b_{chamber}$	15.0†	-1.8	1136.6†		14.5†	
b_{linear}	67.5	190.7	2486.9		93.6	
$b_{quadratic}$	NS	-0.1	NS		-0.06	
R^2	0.99	0.99	0.97		0.98	

‡ Ambient plot (no chamber).

¶ s_x and CV (%) from ANOVA.

§ Curves were fitted against actual CO_2 values. Note: Linear and quadratic coefficients should be multiplied by 10^{-3}.

† Significant F (0.95 level) for chamber effect.

Leaf area at anthesis increased with CO_2 enrichment in both water treatments (Table 2). There was no stress by CO_2 treatment interaction; plants in both water treatments responded to elevated CO_2 similarly. At pod fill we observed a stress by CO_2 treatment interaction (Table 3). Despite a reduction in leaf area due to water stress, the proportional increase in leaf area due to CO_2 enrichment was greater for WS plants since additional CO_2 had no significant effect on leaf area of WW plants. This interaction could have been the result of less rapid rate of leaf expansion in WS plants compared to WW plants between 63 and 98 days after planting under CO_2 enrichment. The WW

Table 3. Mean total dry weight, leaf area, and pod dry weight for soybeans grown under two water regimes in open plots and five CO_2 treatments within chambers at 98 days after planting (well-watered = WW, water-stressed = WS).

CO_2 (μLL^{-1})	Dry Wt. (g)		Leaf Area (cm^2)		Pod Dry Wt. (g)	
	WW	WS	WW	WS	WW	WS
348‡	131.4	101.5	7873	6327	39.3	31.4
349	181.2	102.8	9365	7182	47.5	30.3
421	230.0	122.0	11114	8231	53.5	33.4
496	204.4	142.6	9931	8860	51.1	35.8
645	228.9	168.9	10476	9611	52.1	42.6
946	239.5	198.8	9939	9468	68.6	55.8
s_x¶	9.3		445.1		2.6	
CV (%)	7.9		7.8		7.7	
b_0§	108.2	45.0	7872.8	98.8	29.1	15.1
$b_{chamber}$	39.8†		2292.2†	940.3†	3.3	
b_{linear}	114.6		NS	23139.2	38.1	
$b_{quadratic}$	NS		NS	-15.1	NS	
R^2	0.97		NS	0.99	0.99	

‡ Ambient plot (no chamber).

¶ s_x and CV (%) from ANOVA.

§ Curves were fitted against actual CO_2 values. Note: Linear and quadratic coefficients should be multiplied by 10^{-3}.

† Significant F (0.95 level) for chamber effect.

plants may have reached their maximum leaf area before 14 weeks whereas leaf area expansion for WS plants continued until week 14.

The higher CO_2 concentration delayed anthesis (and shortened its duration) by about 2 days under both water treatments. Other investigators have reported a delay in anthesis for soybean due to CO_2 enrichment (Hesketh and Hellmers, 1973; Rogers et al., 1984a). Water stress had little effect on the timing of anthesis regardless of CO_2 level. Despite the shorter flowering period, high CO_2 grown plants probably had fewer flower abortions since increases in pod number were observed for both water treatments at pod fill (data not shown) and at maturity harvest (Table 4). The extra CO_2 extended pod

Table 4. Mean total pod number, pod dry weight, and weight per pod for soybeans grown under two water regimes in open plots and five CO_2 treatments within chambers at maturity (well-watered = WW, water-stressed = WS).

CO_2 (μLL^{-1})	Pod Number		Pod Dry Wt. (g)		Wt. Per Pod	
	WW	WS	WW	WS	WW	WS
348‡	163	128	64.4	58.2	0.40	0.46
349	186	118	82.8	62.1	0.45	0.53
421	226	127	101.9	73.8	0.45	0.58
496	211	142	92.2	73.8	0.44	0.52
645	205	156	90.3	74.8	0.44	0.48
946	219	157	93.5	72.8	0.43	0.46
s_x	5.5		4.2		0.01	
CV (%)	7.1		6.8		5.3	
b_0	153.5	34.3	64.4	58.2	0.40	0.51
$b_{chamber}$†	14.8	-12.2	27.7†	13.2†	0.04†	0.09†
b_{linear}	26.7	344.4	NS	NS	NS	-0.16
$b_{quadratic}$	NS	-0.2	NS	NS	NS	NS
R^2	0.84	0.99	NS	NS	NS	0.74

‡ Ambient plot (no chamber).

¶ s_x and CV (%) from ANOVA.

§ Curves were fitted against actual CO_2 values. Note: Linear and quadratic coefficients should be multiplied by 10^{-3}.

† Significant F (0.95 level) for chamber effect.

filling by ~3 days; the increases in pod dry weight seen under both water treatments (i.e., at the pod fill sampling) may have been due to this longer pod filling period. Duration of seed filling remained unchanged at high CO_2, but was shortened by 2 days due to water stress.

The overall effects of CO_2 and water treatment on yield components are shown in Table 3 (pod fill). Water stress reduced both pod dry weight (Table 3) and pod number (data not shown) at all CO_2 level. Increases in pod dry weight due to CO_2 enrichment were observed under both water regimes; pod dry weight increases for WW plants may be due to an increase in weight per pod, while more pods per plant was responsible for pod dry weight increases under WS conditions.

The number of pods produced at maturity (Table 4) was slightly greater under CO_2 enrichment. Water stress reduced pod production at maturity. However, the relative increases in pod and seed number in response to additional CO_2 were greater for plants grown under water stress. An increase in pod number resulted in a greater number of seeds per plant (Table 5), but there was only a small nonsignificant increase in pod dry weight with increasing CO_2 concentration (at both water levels). Weight per pod declined with increasing CO_2 under WS conditions but remained constant under WW conditions across the various CO_2 levels. Weight per seed increased slightly in response to water stress and decreased in response to CO_2, especially under stress conditions.

Our present observations indicate only 9% and 12% nonsignificant increases in seed dry weight for WW and WS plants, respectively, at 946 vs 349 μLL^{-1} CO_2. Other studies have reported that CO_2 enrichment increased soybean pod number but this did not necessarily guarantee an increase in pod dry weight (Rogers et al., 1984a; 1986); CO_2 yield responses in terms of seed number and seed dry weight were not reported in these studies. Other studies have found that increases in seed yield observed under CO_2 enrichment were associated with greater numbers of seeds per plant, with seed size remaining constant or increasing slightly (Gifford, 1979; Sionit et al., 1981; Jones et al., 1984a; Rogers et al., 1983a). These different responses to CO_2 enrichment may have occurred because of differences in the availability of mineral nutrients.

In our study, the small yield response to elevated CO_2 may have been related to an inadequate supply of phosphorus. Generally, a P level of greater than 0.25% for leaves sampled at anthesis (Hanway and Olson, 1980) or early pod set (Jones et al., 1991) is sufficient. In this study, leaf analysis at anthesis showed a decrease in P concentration of ~33% at the high CO_2 level; the P concentration for WW and WS treatments were 0.24% and 0.30% at 349 μLL^{-1} CO_2 and 0.16% and 0.20% at 946 μLL^{-1} CO_2, respectively. Prior investigations have found that plants grown under CO_2 enrichment exhibit reductions in the concentration of nutrients in plant tissue (Conroy, 1992; Conroy et al., 1992; Porter and Grodzinski, 1989; Rogers et al., 1984a). In the present study, the application rate of only one liter per week of nutrient solution (containing 0.25 mM of P) coupled with a low P level in the soil may not have been sufficient to meet the P requirement of the

Table 5. Mean seed number, seed dry weight, and weight per seed for soybeans grown under two water regimes in open plots and five CO_2 treatments within chambers at maturity (well-watered = WW, water-stressed = WS).

CO_2 (μLL^{-1})	Seed Number		Seed Dry Wt. (g)		Wt. Per Seed	
	WW	WS	WW	WS	WW	WS
348‡	319	272	46.1	40.8	0.14	0.15
349	409	254	53.5	41.1	0.13	0.16
421	478	275	65.5	50.0	0.14	0.18
496	465	302	58.1	48.0	0.13	0.16
645	441	341	57.4	48.2	0.14	0.14
946	529	379	57.8	45.7	0.11	0.12
s_x¶	26.2		2.8		0.008	
CV (%)	11.5		6.7		8.9	
b_0§	269.4	199.6	46.1	40.8	0.16	0.18
$b_{chamber}$	113.5†	-8.3	14.8†	5.8†	-0.009†	0.02†
b_{linear}	141.6	207.6	NS	NS	-0.04	-0.09
$b_{quadratic}$	NS	NS	NS	NS	NS	NS
R^2	0.88	0.97	NS	NS	0.91	0.90

‡ Ambient plot (no chamber).

¶ s_x and CV (%) from ANOVA.

§ Curves were fitted against actual CO_2 values. Note: Linear and quadratic coefficients should be multiplied by 10^{-3}.

† Significant F (0.95 level) for chamber effect.

larger CO_2-enriched plants. This P level may have been sufficient initially since the total pod dry weight at the pod fill sampling increased significantly with increasing CO_2 concentration (Table 3). However, as the season progressed the demand for P probably increased and altered assimilate translocation to the seeds, thus resulting in the small nonsignificant seed yield increase observed at maturity (Table 5). Studies conducted with soybeans grown under ambient CO_2 concentration and various levels of phosphorus demonstrated that the P level used in our study (0.25 mM) was in the low to intermediate range in terms of yield response (Israel, 1987). Giaquinta et al. (1981) reported that increasing the nutrient phosphate concentration decreased the starch/sucrose ratio which in turn increased the dry matter accumulation in the seeds. Cure et al. (1988) suggested that under P limiting conditions, N_2-fixing plants may not be as responsive to extra CO_2 with respect to growth and yield as plants dependent on inorganic sources of N.

In contrast to results reported here, greater yield increases due to CO_2 were reported for those studies which had more frequent applications of nutrient solution (Sionit et al., 1981), adequate rates of fertilizer applied to the soil (Gifford, 1979; Jones et al., 1984; Rogers et al., 1984a), and unrestricted soil volume for root development and exploration of available nutrients (Jones et al., 1984; Rogers et al., 1986). The discrepancies between these findings and ours indicate the importance of considering fertility requirements of crops in a CO_2-enriched environment.

Another important factor which may have contributed to the small CO_2 yield response observed in our study could be related to root restriction which may have limited photosynthetic capacity of pot grown plants (i.e., sink limited feedback inhibition) (Sionit et al., 1984; Arp, 1991; Thomas and Strain, 1991). Root restriction within field soil profiles can also occur (e.g., traffic induced soil compaction, tillage and natural hardpans, etc.). Therefore, results of containerized studies may in some cases reflect responses of plants growing in the field. This suggests a need to conduct CO_2 studies in the field under different tillage systems and with different soil series.

The harvest index decreased with elevated CO_2 and increased under chronic water stress conditions (Table 6). Seed oil content was observed to increase slightly with increasing CO_2. Elevated CO_2 had no effect on the fatty acid composition of the seed oil (data not shown). There was a trend toward decreasing seed protein value with increasing CO_2. These findings are in general agreement with observations reported by Rogers et al. (1984a). In the present study, water stress had no significant effect on either seed oil or protein values.

Despite the small yield response to CO_2, increased total dry matter production due to CO_2 under both water regimes represents more carbon fixed and in turn more carbon input to the soil. This input may influence carbon storage/cycling as well as belowground physical and biological processes. More dry matter returned to the soil surface may also be important for erosion control in light of the increasing adoption of conservation tillage. At present, CO_2 field studies have only begun to consider these topics.

Table 6. Mean total dry weight, harvest index, and total oil (%) for soybeans grown under two water regimes in open plots and five CO_2 treatments within chambers at maturity (well-watered = WW, water-stressed = WS).

CO_2 (μLL^{-1})	Dry Wt. (g)		Harvest Index		Total Oil (%)	
	WW	WS	WW	WS	WW	WS
348‡	91.1	79.8	0.57	0.56	20.4	20.5
349	128.4	92.6	0.49	0.53	21.2	20.7
421	157.5	104.0	0.48	0.54	21.8	21.4
496	148.9	106.1	0.46	0.49	22.0	21.5
645	156.8	117.6	0.43	0.49	20.9	21.4
946	156.3	117.0	0.43	0.45	21.1	21.0
s_x¶	7.4		0.0006		0.16	
CV (%)	5.8		2.7		2.1	
b_0§	80.7	67.3	0.70	0.67	19.2	
$b_{chamber}$	51.9†	20.3†	-0.08†	-0.03†	0.80†	
b_{linear}	29.7	36.0	-0.48	-0.36	5.1	
$b_{quadratic}$	NS	NS	0.003	0.0002	-0.0043	
R^2	0.94	0.93	0.99	0.97	0.83	

‡ Ambient plot (no chamber).

¶ s_x and CV (%) from ANOVA.

§ Curves were fitted against actual CO_2 values. Note: Linear and quadratic coefficients should be multiplied by 10^{-3}.

† Significant F (0.95 level) for chamber effect.

Growth Analysis

The net assimilation rate (NAR) and relative growth rate (RGR) over three time intervals (5 to 14 days, 14 to 63 days and 63 to 98 days) during the growing season are given in Fig. 1. Data shown for the initial interval are mean values under WW conditions since no water stress had been imposed during this period, whereas the latter two intervals include data for both WW and WS treatments.

The effects of CO_2 enrichment on NAR were dependent on plant age, length of exposure, and water treatment (Fig. 1A). During the first interval (5 to 14 days), NAR (an approximate measure of leaf C-assimilatory capacity) was observed to increase with increasing atmospheric CO_2 concentration. The highest value of NAR (19.14 g m^2 day^{-1} at 946 μLL^{-1} CO_2) was 33% greater compared to the 349 μLL^{-1} CO_2 treatment level. In another open top chamber study, soybean sampled over a similar time interval showed an NAR increase of 67% due to CO_2 enrichment (Rogers et al., 1984a). Growth chamber CO_2 studies conducted with wheat showed similar changes in NAR (Neales and Nicholls, 1978; Sionit et al.,1979).

In this study, the maximum NAR enhancement due to CO_2 enrichment was observed during the second interval (weeks 2-9). Net assimilation rate increased 53% at the 946 μLL^{-1} CO_2 under WW conditions. Although water stress reduced NAR more at higher CO_2 levels (645 to 946 μLL^{-1} CO_2), NAR was increased by ~35% at these CO_2 treatments relative to ambient conditions. By the third interval (weeks 9-14) NAR was relatively constant across CO_2 treatments under WW conditions. The highest value of NAR for WS plants (3.4 g m^2 day $^{-1}$ at 946 μLL^{-1} CO_2) was 46% greater than at 349 μLL^{-1} CO_2.

Increasing the CO_2 concentration had the greatest effect on RGR during the first interval (Fig. 1B). Initial increases in RGR under elevated CO_2 were attributed to increased NAR (Fig. 1A). As with NAR, RGR decreased at each CO_2 value as the plants aged, especially between the second and third interval. The initially high values of RGR and NAR observed during earlier phases of growth followed by a gradual decline with plant age (ontogenetic drift; Kvet et al., 1971) are consistent with those reported for soybean under ambient CO_2 conditions (Koller et al., 1970).

Despite increased NAR due to higher CO_2 during the second interval, RGR values for both WW and WS plants were only slightly higher under higher CO_2. RGR under WS conditions was equally reduced at the various CO_2 concentrations, thus the CO_2 response was similar to that observed under WW conditions.

For the third interval, we detected a decrease in RGR under WW conditions, whereas WS values for RGR remained fairly constant despite increasing CO_2 concentration. The greatest reduction of RGR for WW plants (41%) was observed when the CO_2 concentration was increased from 349 to 946 μLL^{-1}. Several investigators have reported that both RGR and NAR were initially increased during early development but declined as plants grew older, especially with further exposure to elevated CO_2 (Huges

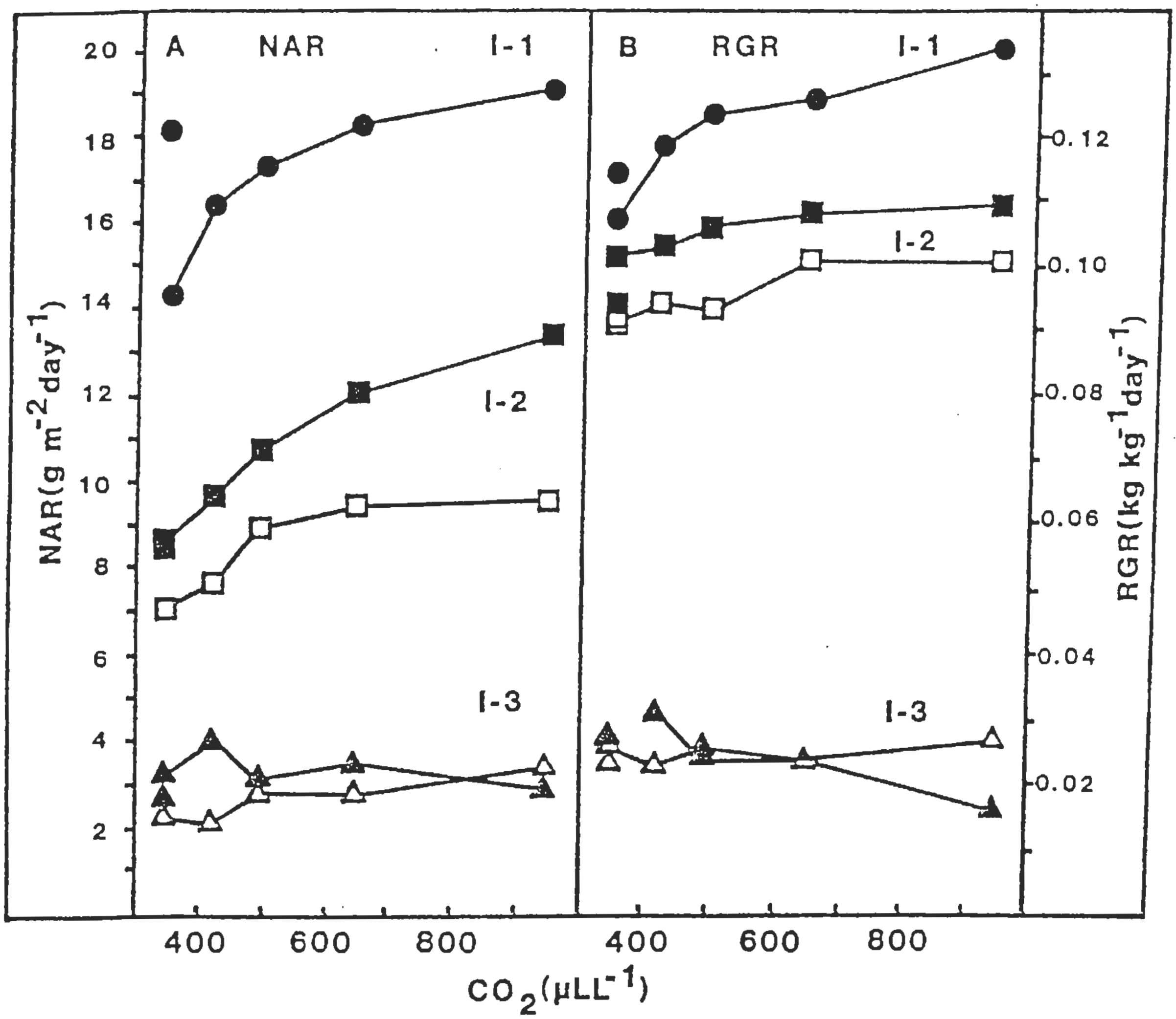

FIGURE 1. Mean NAR and RGR for well-watered (closed symbols) and water-stressed (open symbols) soybean grown in open plots (lone symbols) and five CO_2 treatments within chambers (connected symbols) at three time intervals [I1 = 5 to 14 days (○,●); I2 = 14 to 63 days (□,■); I3 = 63 to 98 days (△,▲) after planting].

and Freeman, 1967; Hurd, 1968; Huges and Cockshull, 1969; Neales and Nicholls, 1978; Rogers et al., 1984a; Tolley and Strain, 1984).

The effects of CO_2 enrichment and water treatment on leaf area ratio (LAR) and its two components, specific leaf area (SLA) and leaf weight ratio (LWR), are shown in Figure 2. Since the stress treatment was not initiated until 2 weeks (after emergence), data for this period represent WW mean values only (Fig. 2A). In general, the distribution of plant dry matter to photosynthetically active tissue (LAR) declined with time and values of LAR at 349 μLL^{-1} CO_2 were invariably greater than those found at

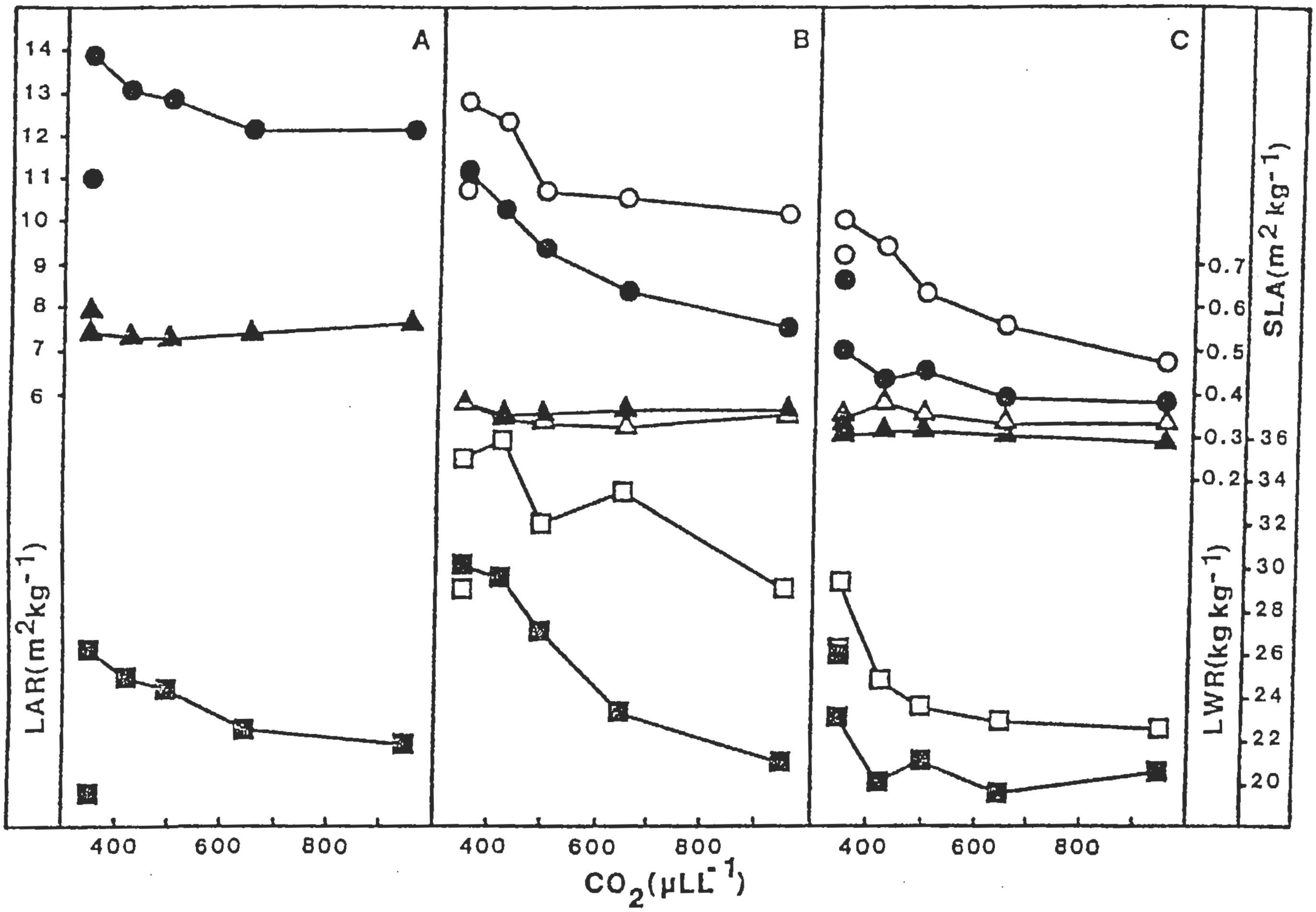

FIGURE 2. LAR (○,●), SLA (□,■) and LWR (△,▲) for well-watered (closed symbols) and water-stressed (open symbols) soybean grown in open plots (lone symbols) and five CO_2 treatments within chambers (connected symbols) at 14 (A), 63 (B) and 98 (C) days after planting.

increased levels of CO_2. As reported by other investigators for several species (Huges and Freeman, 1967; Hurd, 1968; Neales and Nichols, 1978; Patterson and Flint, 1980; Rogers et al., 1984a; Tolley and Strain, 1984), this reduction in LAR was not attributed to a change in dry matter allocation to the leaves (LWR) but to a reduction in leaf area per unit leaf dry weight (SLA). Differences in LWR were small at the various CO_2 concentrations at each harvest; LWR decreased from day 14 to 63 and then remained relatively constant thereafter. Reduction of SLA with increasing CO_2 was clearly evident at each harvest, with the highest SLA values being observed at day 63; the decrease in SLA under high CO_2 may be attributed to a greater starch accumulation in the leaves (Patterson and Flint, 1980; Madsen, 1968) and/or to an increase in leaf thickness (Hurd, 1968; Thomas and Harvey, 1983).

Although LAR was depressed by CO_2 enrichment under both water treatments, the LAR of WS plants was always higher than LAR of WW plants at each CO_2 level (Fig. 2B and 2C). At day 63, over half of the decrease in LAR of WS plants occurred over the range 349 to 496 μLL^{-1} CO_2, with the greatest decrease being observed at 946 μLL^{-1} CO_2 (Fig. 2B). Under WW conditions, the decrease in LAR from 349 to 496 μLL^{-1} CO_2 were very similar to the WS response, and the LAR values of WS plants were about 15% greater than their WW counterparts. The greater reduction in LAR for WW plants at 645 and 946 μLL^{-1} CO_2 resulted in larger differences between values for WW and WS plants at these CO_2 levels. At day 98, LAR of WS plants was decreased by 33% when CO_2 was increased from 349 to 946 μLL^{-1} (Fig. 2C). Under WW conditions, reductions in LAR were less dramatic over the CO_2 concentration range. At this harvest, the greatest differences between water treatments were observed under low CO_2 and diminished when CO_2 was raised. LAR for WS plants at 349 to 421μLL^{-1} CO_2 were about 46% greater than values for WW plants, whereas LAR at 946 μLL^{-1} CO_2 was only 16% greater. Reduction of SLA with increasing CO_2 was responsible for the reductions in LAR observed at each harvest. Conversely, LWR remained relatively constant with increasing CO_2. Differences due to water treatment were not great at 63 days after planting, and although LAR values for WS plants at 98 days after planting were invariably greater than values for WW plants, the differences were not large.

The observed reductions in LAR coupled with changes in NAR are important because these are the two component growth parameters of RGR (Figures 1 and 2). At the first interval, the opposing effect of LAR on NAR was not great since RGR was enhanced when the CO_2 concentration was raised from 349 to 946 μLL^{-1}. However, for the second interval, the reduction in LAR was large enough to depress RGR under both water treatments despite significant increases in NAR at high CO_2. Note that LAR offset NAR more under WW conditions, thus accounting for the similar responses of RGR to CO_2 for WW and WS plants. At the third interval, a fairly constant NAR coupled with reduced LAR resulted in the RGR for WW plants being depressed at the higher CO_2 concentrations (496 to 946 μLL^{-1}). In contrast, the RGR of WS plants remained essentially unchanged under higher CO_2 since increases in NAR were neutralized by decreases in LAR. Several investigators have reported similar changes in time for RGR through adjustments of NAR and LAR under elevated CO_2 concentration (Huges and

Freeman, 1967; Hurd, 1968; Neales and Nichols, 1978; Huges and Cockshull, 1969; Rogers et al., 1984a).

CONCLUSION

Increasing the CO_2 concentration had no effect on dry weight growth at the seedling stage. This result, contrary to the expected response, may have been due to competition since each container had more than one plant up until the 14 day after planting harvest. Thus, although NAR and RGR for the first interval increased with increasing CO_2 concentration, these increases were not as great as those frequently observed during early developmental growth. Later in the season (anthesis and pod fill samplings), CO_2 enrichment did significantly increase total dry weight. Water stress inhibited growth at all CO_2 levels at both periods. However, the relative enhancement of growth due to increasing CO_2 concentration under WS conditions was as great or greater than that under WW conditions. At each of these periods, increasing the CO_2 concentration was observed to have a compensating effect for water stress. For both periods, WS plants grown under 946 μLL^{-1} CO_2 were larger than WW plants grown under 349 μLL^{-1} CO_2. This compensating effect was due to the fact that WS plants under high CO_2 had growth characteristics (i.e., RGR, NAR, and LAR) similar to WW plants under ambient CO_2.

Reproductive yield increases due to CO_2 enrichment were represented by a significant rise in seed number. Although water stress had an adverse effect on yield, the relative increase in seed number in response to elevated CO_2 was greater for WS plants. There was a significant decrease in weight per seed with CO_2 under both water treatments. There was only a trend toward increase in total seed dry weight. This leads us to suggest that a limiting P supply and/or a restricting soil environment may have led to the lack of a significant seed yield response to increasing CO_2. Further research with crops grown in the field using different irrigation, fertility and tillage management practices, and different soils is needed if we are to develop a reliable knowledge base that will allow prediction of crop response in a future higher CO_2 world.

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